

Body shape-shifting during growth permits tests that distinguish between competing geometric theories of metabolic scaling

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29

30 **Abstract**

31 Metabolism fuels all of life's activities, from biochemical reactions to ecological interactions.
32 According to two intensely-debated theories, body size affects metabolism via geometrical
33 influences on the transport of resources and wastes. However, these theories differ crucially
34 in whether the size-dependence of metabolism is derived from material transport across
35 external surfaces, or through internal resource transport networks. We show that when body
36 shape changes during growth, these models make opposing predictions. These models are
37 tested using pelagic invertebrates, because these animals exhibit highly variable intraspecific
38 scaling relationships for metabolic rate and body shape. Metabolic scaling slopes of diverse
39 integument-breathing species were significantly positively correlated with degree of body
40 flattening or elongation during ontogeny, as expected from surface-area theory, but
41 contradicting the negative correlations predicted by resource-transport-network models. This
42 finding explains strong deviations from predictions of widely-adopted theory, and underpins
43 a new explanation for mass-invariant metabolic-scaling during ontogeny in animals and
44 plants.

45 (150 words)

Introduction

The speed of metabolism, or the rate at which organisms transform resources into biological work and structures, has profound physiological, ecological and evolutionary implications (Brown *et al.*, 2004; Kooijman, 2010; Sibly *et al.*, 2012). In aerobic organisms, this process can be estimated by aerobic respiration (R), which is typically related to body mass (M) using a power function, $R = aM^b$. Debates that started over 75 years ago about how to predict the value of the respiration scaling exponent b (henceforth b_R) (Brody, 1945; Kleiber, 1961; Brown *et al.*, 2004; Makarieva *et al.*, 2008), have recently become very intense, as contrasting theories compete to explain variation in rates of metabolism of different-sized organisms (West *et al.*, 1999; Kozlowski *et al.*, 2003; Banavar *et al.*, 2010; Dodds, 2010; Glazier, 2010; Kooijman, 2010; Price *et al.*, 2012).

Two groups of theories that predict metabolic rates based on geometrical relationships between body mass and resource supply (or waste removal) have become prominent. These theories differ crucially in whether metabolic scaling is assumed to be more strongly influenced by transport of materials through external exchange surfaces such as those of skin, lungs and gills (“Surface Area” or SA theory) (Rubner, 1883; Kooijman, 2010; Okie, 2013), or by physical and geometrical properties of internal networks for transport of materials, including animal and plant vascular systems (“Resource Transport Network” or RTN theory) (West *et al.*, 1999; Savage *et al.*, 2008; Banavar *et al.*, 2010). A major empirical challenge has been to distinguish between the very similar metabolic (respiration) scaling exponents predicted by various SA and RTN models (Kearney & White, 2012). SA theory, which invokes Rubner’s (1883) surface law applied to surfaces that exchange energy or materials, predicts that when size increase involves no change in body shape, surface area will decline relative to volume or mass. Thus, the simplest SA theory, which assumes that respiration rate is proportional to the surface area of an isomorphically growing organism (i.e. which retains

its relative shape), predicts that $b_R = 2/3$. Alternatively, models based on the geometry of resource-transport networks predict a slightly higher b_R value of $3/4$ (West *et al.*, 1999; Banavar *et al.*, 2010), though this value may vary depending on network properties (Price *et al.*, 2007; Savage *et al.*, 2008; Banavar *et al.*, 2010; Dodds, 2010; Price *et al.*, 2012). A second outstanding challenge has been for these general theories to account for substantial and systematic deviations from these predictions, as occurs during the ontogeny of diverse animals and plants, including cases where b_R -values are near, and sometimes greater than 1 (Glazier, 2005, 2006).

Here, we overcome both of these challenges by performing a test that clearly distinguishes between predictions of SA- and RTN-models. Our test is powerful because it exploits the greater divergence in the predictions of these models when growth is associated with large body-shape changes (see also Kearney and White, 2012), and it uses the most comprehensive set of intraspecific measurements of pelagic invertebrate body-shape change and metabolic scaling collected to date. Pelagic animals are ideal for this test, because they are physiologically and taxonomically diverse (occurring in many different phyla), they change shape markedly during ontogeny (Hirst, 2012), show varied intraspecific metabolic scaling exponents (Glazier, 2005, 2006), and commonly exchange oxygen and wastes across large portions of their body surface throughout much or all of their ontogeny (Graham, 1988; Pirow *et al.*, 1999), even in relatively large active species such as cephalopods (Seibel, 2007).

Methods

Euclidean Surface Area Predictions

In order to overcome the challenge posed by the paucity of data on invertebrate body-surface area, and the area of uptake surfaces during ontogeny, we developed a model that relates the smooth surface area–mass scaling exponent b_A to the mass-body length scaling

exponent b_L , extending previous predictions (Okie, 2013) (*Supplementary Information 1*). We
 next apply this Euclidean geometric model to the abundant literature data on body mass-
 length scaling exponents, b_L . These b_L values for ontogenetic growth are least-squares
 regression (LSR) slopes of log body mass against log body length, measured along the long
 body axis, or as the diameter of oblate medusal forms, which all grow primarily by radial
 increase rather than bell-height increase (Hirst, 2012). Given a lack of strong systematic
 variation in mass-density during ontogeny, relative to size increase (see *Supplementary*
Information), we make the reasonable approximation that mass (M) \propto Volume (V) during
 ontogeny. Thus, when body shape remains unchanged during growth (i.e. growth is
 isomorphic), $M \propto V \propto L^3$, and therefore $b_L = 3$ (Fig. 1A). In this case, smooth or Euclidean
 surface area (A) is proportional to $M^{2/3}$, as predicted from Rubner's (1883) surface law, and
 therefore $b_A = 2/3$ (Fig. 1B). To identify limits to Euclidean shape-shifting, consider an
 extreme case of when a body, including its appendages, elongates from an initially miniscule
 size solely along the longest body axis: here at the limit, $M \propto L^1$, hence $b_L = 1$ (Fig. 1A).
 Moreover, it is evident that such pure elongation produces $A \propto L^1$, hence $b_A = 1$ (Fig. 1B).
 Another extreme shape shift results when growth, again from an initially miniscule size,
 occurs in equal proportion, but only in the two longest dimensions (shape flattening); here at
 the limit, $M \propto L^2$, hence $b_L = 2$ and again $b_A = 1$ (Fig. 1). Thus, both elongation and shape-
 flattening during growth reduce b_L below 3, and increase b_A from 2/3 to 1 (Fig. 1). By
 contrast, when body shape becomes more squat (thicker), caused by proportionately less
 growth along the long axis than along the shorter axes (described mathematically in
Supplementary Information 1 Predicting b_A from b_L using Euclidean geometry), $b_L > 3$, with
 possible b_A values somewhat above or below 2/3, depending on the exact nature of the shape
 change (Fig. 1). The contribution of body thickening to Euclidean surface area when size
 increase is dominated by growth in one or both of the longest axes is also discussed in
Supplementary Information 1. Since this geometrical approach to predicting surface-area

scaling accounts for different degrees of growth in different dimensions, it can be applied to any Euclidean body shape and shape change, and it can be compared with actual, rarely measured, surface area changes as well. However, unique values of b_A usually cannot be predicted from b_L . To solve this problem, we used dimensional analysis to define the limits of the surface-area scaling exponents b_A that correspond to body mass-length exponents b_L over a biologically realistic range of shape changes (*Supplementary Information 1*); these boundaries are shown in Fig. 2.

Resource Transport Network Predictions

The model of West *et al.* (1999) predicts that when growth increases proportionately in three dimensions (isomorphic), $b_R = 3/4$, whereas when growth involves proportionate increases in only two dimensions, $b_R = 2/3$, and for growth in only one dimension, $b_R = 1/2$. Another related RTN model, the “radial explosion network” model of Banavar *et al.* (2010) was also extended to consider how body-shape change (estimated as b_L) would alter the predicted scaling of metabolic rate (b_R). Based on different assumptions, this model predicts either the same values as the model of West *et al.* (1999) or somewhat smaller b_R values for 2D and 1D growth ($b_R = 5/8$ and $1/4$, respectively: see *Supplementary Information 2*). Price *et al.* (2007) also claimed that the predictions of the model of West *et al.* (1999) should be modified for relatively small organisms, predicting that b_R should = 1, 0.86 and 0.60 for 3D, 2D and 1D growth, respectively. These predictions were not explicitly considered here because (1) Price *et al.* (2007) did not specify precisely what should be considered a small versus large organism, and (2) our analyses show that b_R is positively correlated with body mass, the opposite of that predicted by the model of Price *et al.* (2007) (see *Supplementary Information 3.5*). In the case of all these RTN models, there is a decline in predicted metabolic scaling exponent as shapes increasingly flatten or elongate. In summary, all current RTN models predict that body elongation or shape-flattening during growth will reduce the

metabolic mass-scaling exponent b_R , whereas SA theory predicts the opposite – that such shape-shifting will increase b_R .

Empirical Data (b_R and b_L)

We obtained b_R values by searching the literature for least-squares regressions of \log_{10} respiration rate *versus* \log_{10} body mass during ontogeny of pelagic marine and freshwater invertebrates at controlled constant temperatures. Routine metabolic scaling datasets were screened to remove less reliable regressions having correlation coefficients (r) below 0.8. Additional screening that excluded regressions with body-size ranges less than an order of magnitude did not materially alter our findings (*Supplementary Information 3*). We also discounted mass-type as driving the observed relationship between b_L and b_R (*Supplementary Information 3*).

To characterize ontogenetic shape change in a single statistic, we used mass-length exponents (b_L), adding to the b_L dataset of Hirst (2012) and following his methodology for screening by correlation coefficients. The higher than predicted b_R values were not due to choice of regression model, as Reduced Major Axis regressions would increase these values further (*Supplementary Information 3*). To avoid systematic over-representation of commonly measured species, species means for b_R and b_L were derived, and these used to calculate means for taxonomic groups listed in Table S2. Our Euclidean surface-area model (Fig. 2 and *Supplementary Information 1*) and the radial explosion network model (Fig. 3 and *Supplementary Information 2*) both predict linear relations between b_R and $1/b_L$, so we performed all regressions using $1/b_L$. As errors are expected to be of similar magnitude for both metabolic and shape changes, and because the evolution of each depends on the other, the scaling exponent b_R was related to $1/b_L$ using Reduced Major Axis regression (Figs. 3 and 5). We searched the literature for direct measurements of surface area-mass scaling exponents (b_A) so that these could be compared with b_A values predicted from Euclidean geometry for a

smooth surface. Appropriate data for b_L and measured b_A values were available for just three aquatic species, the euphausiid *Thysanoessa raschii* (Harding, 1977), the amphipod *Gammarus zadacchi* (Wang & Zauke, 2002), and the scyphomedusan *Aurelia aurita* (Deighton, 2013). The surface area of *G. zadacchi* was estimated indirectly by an acid-base titration method (Wang & Zauke, 2002), and was considered to equal both internal and external surfaces permeable to ions (and thus may include cell membrane surfaces). All these values are presented in Fig. 4, showing how in each case the Euclidean prediction of surface scaling is lower than that achieved, hence suggesting an increase in the fractal dimension of the surface during ontogeny (including the addition of limbs and surface convolutions).

Results

To illustrate the contrasting predictions between the SA- and RTN-models, consider the extremes of shape flattening and pure elongation during growth compared with no shape change (isomorphy). Values of b_L are 3 for isomorphic growth, and approach 2 for shape flattening, and 1 for pure elongation (Fig. 1A). For the latter two extremes, $A \propto M^1$ (i.e. $b_A = 1$), hence a match between surface area and metabolic scaling would predict $b_A = b_R = 1$ (Figs. 1B and 2). In stark contrast, existing resource-transport network models predict the opposite effect of shape change on b_R : for equal proportional length increases in just two dimensions, b_R is reduced to either $\frac{2}{3}$ (West *et al.*, 1999) or even $\frac{5}{8}$ using a more recent model (Supplementary Information 2); and for pure elongation b_R is reduced further to $\frac{1}{2}$ (West *et al.*, 1999), or to $\frac{1}{4}$ (Supplementary Information 2).

To make full use of the b_R values from 237 regressions for 89 pelagic invertebrate species, and the b_L values from 580 regressions for 259 species, we first show, among 12 taxonomic groups that have distinct body forms and characteristic mass-length (Hirst, 2012) and respiration-mass scaling (Glazier, 2005) (Fig. S2), that taxon-mean b_R is positively correlated with mean $1/b_L$ ($r^2 = 0.60$; $p < 0.004$; Fig. 3A). This result is also reinforced by a

similar regression obtained across 70 species-specific values ($r^2 = 0.37$; $p = 0.00000002$; Fig. 3B).

Intriguingly, the predicted surface-area scaling exponents (b_A) derived from b_L values (between the upper and lower blue lines in Fig. 3A) are below the observed mean b_R values. A resolution of this discrepancy is suggested by examining rare measurements of surface areas throughout the ontogeny of two crustaceans and a scyphomedusan, which included surface convolutions from gill development, additional appendages and other surface “frills” (hence fractal dimension) (Okie, 2013). These actual measurements showed steeper scaling with body mass than did Euclidean estimates (Fig. 4), thereby supporting the argument that fractal dimension of the uptake surface scales positively with mass. Notably, chaetognaths with simple, smooth body surfaces throughout ontogeny have the lowest b_R values, closest to predicted b_A values (Fig 3A). Our findings therefore show that shape-shifting during ontogenetic growth among phylogenetically and morphologically diverse pelagic invertebrates accounts for substantial deviation from $3/4$ - or $2/3$ -power scaling (Glazier, 2005, 2006) in the direction predicted by theories based on surface-area influences (blue lines in Fig. 3A), but in the opposite direction predicted by existing RTN models (red lines in Fig. 3A). To distinguish clearly between opposing predictions of these SA and RTN models, we next focus on the range of body-shape changes over which their predictions are in opposite directions. This range encompasses the majority of species, whose shape change is characterized by $b_L \leq 3$.

Further support for the role of a permeable surface area in explaining metabolic scaling comes from a comparison of taxa with and without an impervious external surface covering. The strength of the relation between metabolic scaling and mass-length change differed among five phyla (ANCOVA; $1/b_L$: $F_{1,45} = 18.54$, $p < 0.0005$; Phylum: $F_{4,45} = 3.53$, $p = 0.014$; $1/b_L \times$ Phylum: $F_{4,45} = 3.9$, $p = 0.008$; $r^2 = 0.62$), with chordates showing greater metabolic sensitivity to increasing b_L than arthropods (Fig. 5). In arthropods, shifts to a less

permeable general body surface later in ontogeny or in larger species (Lockwood, 1967), coupled with increased reliance on localised respiratory organs (e.g. gills) may explain why their metabolic scaling shows little sensitivity to body-surface area (Fig. 5).

Values of b_R also tend to be higher in gelatinous than in non-gelatinous taxa, but a General Linear Model analysis of species for which $b_L \leq 3$ showed a stronger effect of $1/b_L$ than of gelatinous categorization (G : gelatinous and semi-gelatinous vs non-gelatinous (Larson, 1986) ($1/b_L$: $F_{1,51} = 7.32$, $p = 0.009$; G : $F_{1,51} = 2.46$, $p < 0.097$; see also *Supplementary Information 3.4 Effects of body composition*). Overall, therefore, the negative relationship between b_R and b_L paralleled the predicted effect of the scaling of permeable surface area (Figures. 3A, 5).

Discussion

The observed increase in b_R with increased shape-shifting, as represented by a reduction in the mass-body length scaling exponent, b_L , was consistent not just with our SA-model, but also with the more detailed dynamic energy budget (DEB) theory of Kooijman (1986, 2010; Maino *et al.*, 2014). In DEB theory, maintenance metabolism is proportional to structural volume (which is the overall volume minus volume of non-metabolizing “reserve”), and total metabolic rate combines maintenance cost of this structure and, the overhead costs of growth (and assimilation), and potentially also surface-area related costs such as osmotic control. Thus, for isomorphic size increase, DEB theory predicts that metabolic rate during ontogeny should scale with mass raised to a power between 2/3 and 1, depending on the relative weighting of different components of metabolism. Without data on these weightings, we were not able to distinguish DEB predictions for isomorphically growing animals from those of current RTN models. However, for the extreme shape changes at the limits of pure elongation and shape-flattening, both our SA-model and DEB theory predict an isometric relationship between metabolic rate and body mass, because Euclidean

SA is also isometrically related to body mass. Moreover, the findings of two previous studies, which compared the intraspecific size-scaling of metabolic rates of colonial bryozoans of different shapes and growth characteristics (White *et al.*, 2011; Hartikainen *et al.*, 2014), also supported the DEB theory of Kooijman (2010) rather than predictions of the RTN model of West *et al.* (1999). Therefore, the observed increase in b_R with increased shape-shifting towards elongation or shape-flattening is consistent with predictions of SA theory, represented by either the model presented in this paper or DEB theory, but contradicts predictions of current RTN models.

However, delivery of resources and wastes between the external environment and mitochondria throughout the body depend on both the area of exchange surfaces and the design of the transport network within the organism, and both would be expected to be consistent with metabolic scaling relationships with body size. If they were not, a mismatch would arise in material and energy exchange with the environment, especially for resources such as oxygen that are typically stored in only small amounts in bodies. Falsification of predictions of current RTN models is therefore surprising, particularly so because we deliberately chose to test models that not only represent different network geometries (West *et al.*, 1999; Banavar *et al.*, 2010), but also have few specific details and hence potentially wide applicability. Moreover, their predictions were falsified despite being based on observations of diverse animal taxa, including cephalopods with closed cardiovascular systems, as well as other animals with open or no obvious circulatory systems. We therefore need to consider why current RTN models may not predict changes in metabolic rate during ontogenetic growth of aquatic invertebrates when body shape changes.

As resource transport networks must connect to mitochondria distributed throughout the body, RTN models assume that the networks are space-filling. However, we suggest that the geometry of this space-filling may differ fundamentally depending on whether materials are distributed from a central hub (e.g. heart), as assumed in current RTN-models (West *et*

al., 1999; Banavar *et al.*, 2010; Dodds, 2010), or from much of the external surface, which may be a more reasonable assumption for many aquatic invertebrates that respire through their integument and whose shape becomes more elongate or flattened during growth. The functionally important paths within transport networks would therefore be between the external surface and each mitochondrion rather than radiating from a central heart to each mitochondrion. When body shape changes during growth, average path lengths within transport networks that match the distribution of exchange surfaces over the body surface should be expected to respond differently from those in radiating transport networks, thereby producing different size-scaling of both resource transport and metabolic rate. For example, when growth is achieved largely by elongation of body shape, the minimum or mean path lengths from a central heart will scale more closely with body length (l_1 in Fig. 2 and S.I.), but when the network is space-filling from the external surface, these path lengths are expected to scale more closely with the length of the shortest, slowest growing axis (l_3 in Fig. 2 and S.I.). We are currently investigating such modifications to the RTN model of Banavar *et al.* (2010) to try to reconcile RTN model predictions with metabolic scaling data for shape-shifting aquatic invertebrates. Even for some species with closed circulatory systems, such as cephalopods, predictions of current network models based on a single centralised heart may not apply: for example, the squid species in our dataset have several hearts located in different parts of the body (O'Dor & Hoar, 2000). Therefore, our findings suggest the intriguing possibility of a major transition in metabolic scaling in multicellular eukaryotes when respiratory uptake shifts from being widely distributed over the body surface to being more localised in specialised respiratory organs, and that this is also expected to coincide with a shift in the geometry of RTNs.

Hitherto underappreciated shape-shifting effects on external surface area also help to resolve a major contradiction between the conventional prediction that mass-specific metabolic rate should decrease as body size increases, both during ontogeny and

interspecifically, within groups of multicellular eukaryotes (West *et al.*, 1999; Banavar *et al.*, 2010; DeLong *et al.*, 2010), and the surprisingly common observation that metabolic rate is directly proportional to body size, or nearly so. Such near-isometric metabolic scaling is observed not only during the ontogeny of pelagic invertebrates (Glazier, 2005; 2006), as studied here, but also in growing pelagic fish larvae, and during the early ontogeny of other animals and plants (Post & Lee, 1996; Glazier, 2005; Mori *et al.*, 2010). Kooijman (2010) has also argued that the external surface area during the early ontogeny of trees is isometrically related to volume (see also Glazier 2010), which under SA theory (including Kooijman's DEB theory) would predict the near isometric metabolic scaling that is observed (Mori *et al.*, 2010). Banavar *et al.* (2014) link shape change to mass-scaling of metabolic rate as well, but argue that $b_R = 3/4$, regardless of whether growth is isomorphic or whether surface area is linearly related to volume ("trees" in their terminology): this clearly contradicts the effects of shape-shifting that we have observed in pelagic invertebrates. However, the model described by Banavar *et al.* (2014) differs critically from ours and from the data presented in the *Supplementary Information 3*. Specifically, although we did not detect or assume a systematic change in body composition, hence density, as body mass increases, Banavar *et al.* (2014) predict that density scales as $M^{1/4}$ in organisms whose external surface area is linearly related to volume.

To understand the role of shape-shifting in generating near-isometric metabolic scaling, we propose that constraints on the scaling of resource encounter, uptake and internal transport should all be considered. Thus the usual diminishing supply and delivery of limiting resources to mitochondria as body size increases (Palzenberger & Pohla, 1992; Banavar *et al.*, 2010) needs to be overcome. Specifically, over ontogeny the encounter, uptake and internal transport of a limiting resource or resources (e.g. energy and/or oxygen) should be directly proportional to body mass. This can happen in integument-breathing pelagic animals with the capacity for shape-shifting, as described here, because recent work has shown that

potential rates of encounter and consumption of food also scale with body mass nearly isometrically (actually with slightly positive allometry) when food is encountered in a 3-dimensional (e.g. pelagic) environment (Pawar *et al.*, 2012). Therefore, we propose that near-isometric scaling of both oxygen and food uptake permits the evolution of near-isometric scaling of routine metabolism during ontogeny. This situation contrasts with the negatively allometric food uptake (i.e. $b < 1$) observed when encounters are in two dimensions (e.g., non-pelagic and terrestrial consumption) (Pawar *et al.*, 2012). Near-isometric metabolic scaling in pelagic fish larvae is also associated with steep initial scaling of gill-surface area, which then becomes shallower later in life (Post & Lee, 1996). During early ontogeny, fish and other organisms showing isometric metabolic scaling may also rely heavily on integumentary exchange of respiratory gases, which when coupled with shape change, parental resource supplements, or both, can prevent negatively allometric resource encounters (Brody, 1945; Mori *et al.*, 2010). Our data do not allow us to test interspecific scaling exponents, but future tests at this scale may benefit from attention to SA constraints.

Our tests have clearly distinguished between predictions of SA- and existing RTN-metabolic scaling models. However, the relative importance of resource supply, waste removal and metabolic demand in driving the slopes of the scaling relationships that we have observed remains an open question. Further research is needed to determine when and whether: (1) surface-area constrained resource supply (or waste removal) primarily limits the level and scaling of metabolism in integument-breathing organisms, (2) natural selection on vital energy-demanding activities (e.g. growth, reproduction and locomotion) related to specific life-styles and environmental challenges is of primary importance, and this has led to adaptive secondary adjustments in body-shape related surface area and associated resource supply to match size-specific metabolic requirements, or (3) the processes of resource supply and use have coevolved in such a tightly symmorphous way that no one process can be considered the primary driver (Glazier, 2005, 2010; Killen *et al.*, 2010).

In any case, our findings not only resolve major empirical contradictions with predictions of general metabolic scaling theory, but also help to explain why near-isometric scaling of routine metabolism occurs in nature. We can also now better understand why isometric metabolic scaling was not completely replaced by negatively allometric scaling when unicells evolved into multicellular organisms (DeLong *et al.*, 2010), but rather persists in many multicellular species during all or parts of their ontogeny.

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Figure Legends

Figure 1 A. Illustration of Euclidean relationships between body length and mass. When organisms grow isomorphically, they retain their original shape throughout ontogeny, and the slope $b_L = 3$. When the organism becomes more squat during ontogeny, $b_L > 3$; and when growth is proportionally greater along the longest axis, or along the two longest axes, $b_L < 3$. The value of b_L approaches the limit of 1 when growth is solely by elongation, and 2 when growth occurs solely and in equal proportion in the two longest dimensions. **B.** Illustration of various Euclidean relationships between body mass and surface area. When growth is isomorphic $b_A = 2/3$; when growth is by pure elongation along the longest axis, or in equal proportion along just the two longest axes, b_A approaches the limit 1; when growth makes body shape more squat, b_A depends on specific details of shape change (see *Supplementary Information 1*).

Figure 2. Conversions from mass-length exponents (b_L) to surface area-mass exponents (b_A), predicted using Euclidean geometry (*Supplementary Information 1*). M denotes mass, V = volume, A = surface area. The boundaries of the predicted b_A values (shaded area) are described by the four equations given. The points where these boundaries intersect (from left to right) describe size increases from an infinitely small size by pure elongation of the body along l_1 , by enlargement in 2 of 3 body dimensions along l_1 and l_2 , and by isomorphic enlargement (without shape change). These three extremes are illustrated with a medusa and

a copepod. Because the medusa primarily increases its radius, simple elongation along one axis alone is not illustrated.

Figure 3. Respiration-mass scaling exponents (b_R) versus mass-length exponents (b_L) for pelagic invertebrates. **A.** taxon-specific means \pm SEM (RMA regression described by: $b_R = 1.699(1/b_L) + 0.224$). Letters denote the taxa: A, appendicularians; Am, amphipods; E, euphausiids; C, chaetognaths; Ce, cephalopods; Cl, cladocerans; Co, copepods; Ct, ctenophores; H, hydrozoans; Pt, pteropods; S, scyphozoans and T, thaliaceans. Predictions of b_R resulting from effects of body-shape change on the geometry of resource-transport networks, as specified by two theoretical models (West *et al.*, 1999; Banavar *et al.*, 2010) (and *Supplementary Information 2*), are shown in red and brown for $b_L = 3, 2$ and 1. **B.** species-specific means (RMA regression described by: $b_R = 2.358(1/b_L) - 0.027$). In both panels, the Euclidean predicted envelope of b_A in relation to b_L values (on right-hand axis) is shown in blue (see Fig. 2 for details).

Figure 4. Euclidean predicted (cross) and also measured b_A values (circles) are given for the euphausiid *Thysanoessa raschii*, amphipod *Gammarus zadacchi* and scyphomedusan *Aurelia aurita*, with values for individual species joined by a vertical line (Harding, 1977; Wang & Zauke, 2002; Deighton, 2013). For comparison, the conversions from mass-length exponents (b_L) to surface area-mass exponents (b_A), predicted using the Euclidean geometric model developed herein is shown in blue.

Figure 5. Relationship between mass-scaling exponent for routine metabolic rate during ontogeny (b_R) and change in body shape, $1/b_L$, for individual species of pelagic invertebrates. Data (black symbols) apply to species ranging from those with isomorphic growth ($1/b_L = 0.33$) to those whose shape becomes increasingly elongate or flattened. RMA regression line, in black, is drawn through significant trends only ($p < 0.05$). Blue dashed lines denote the predicted maximum and minimum exponents derived from Euclidean surface area increase (*Supplementary Information 1*); solid lines denote predictions from network model of West *et al.* (1999) (brown line) and derived from Banavar *et al.* (2010) (red line). **A.** Chordata; **B.** Mollusca, **C.** Cnidaria, **D.** Ctenophora; **E.** Arthropoda. The observed positive trends are opposite to those predicted by resource transport network theories. The lack of relationship among species of Arthropoda may be related to the development of a relatively impermeable cuticle and localised respiratory organs.

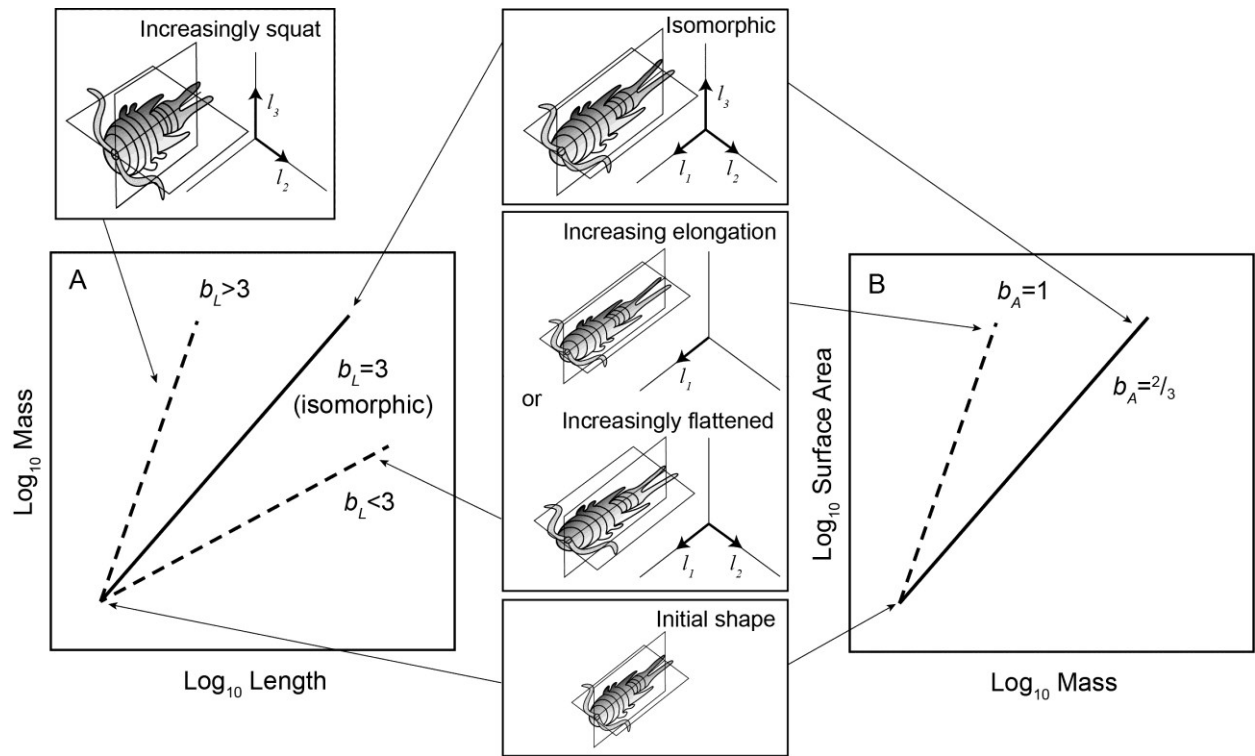


Fig. 1

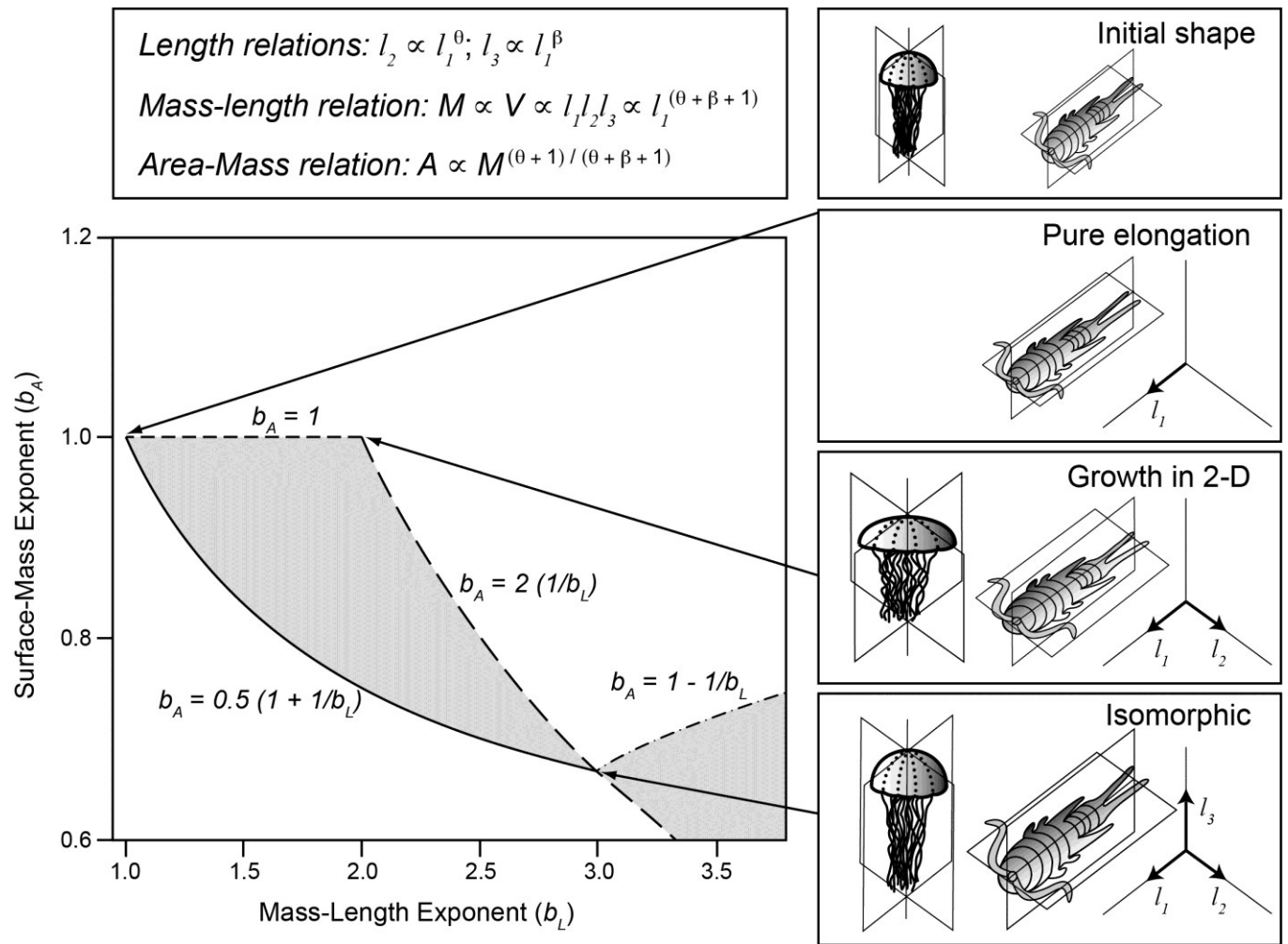


Fig. 2

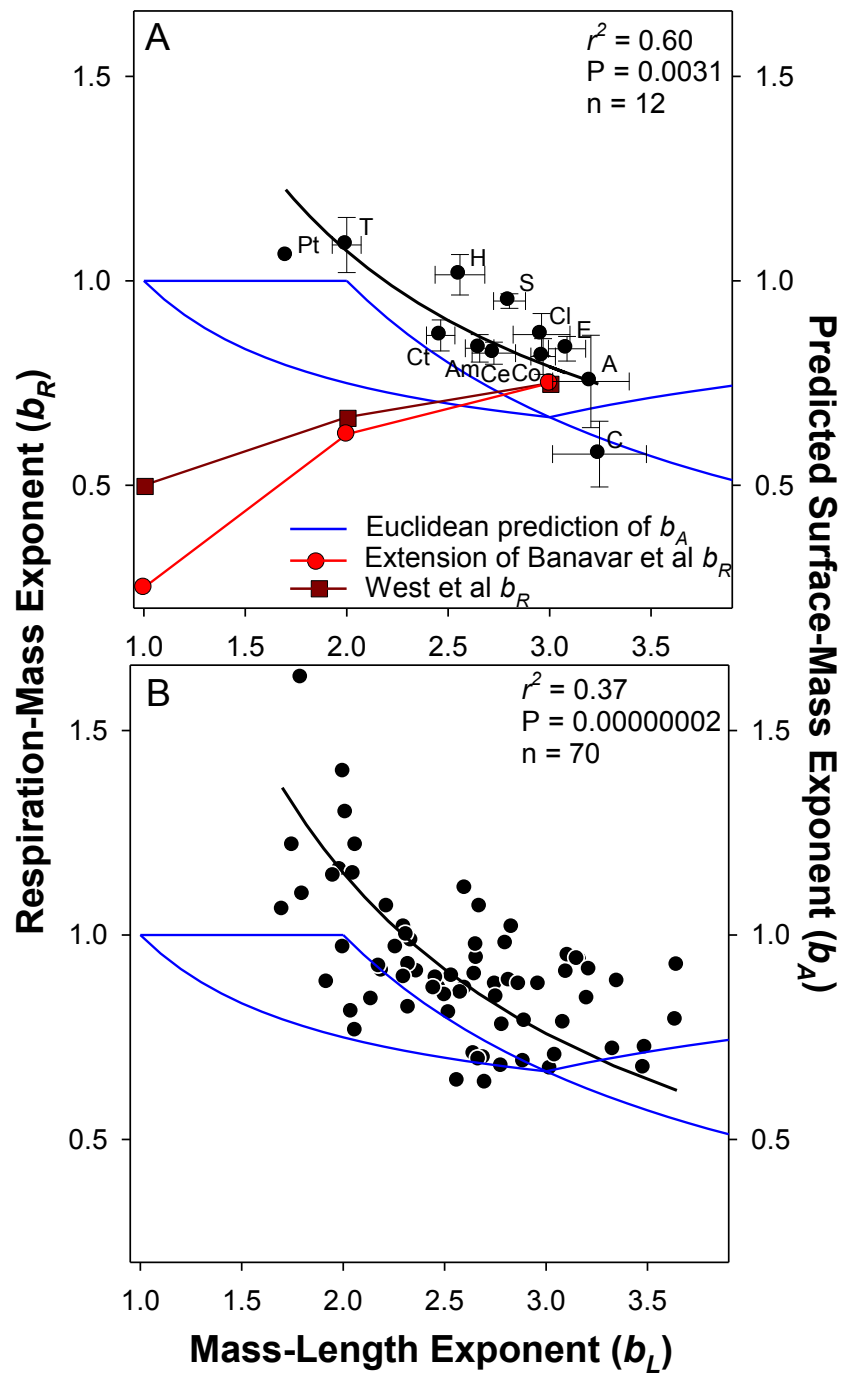


Fig. 3

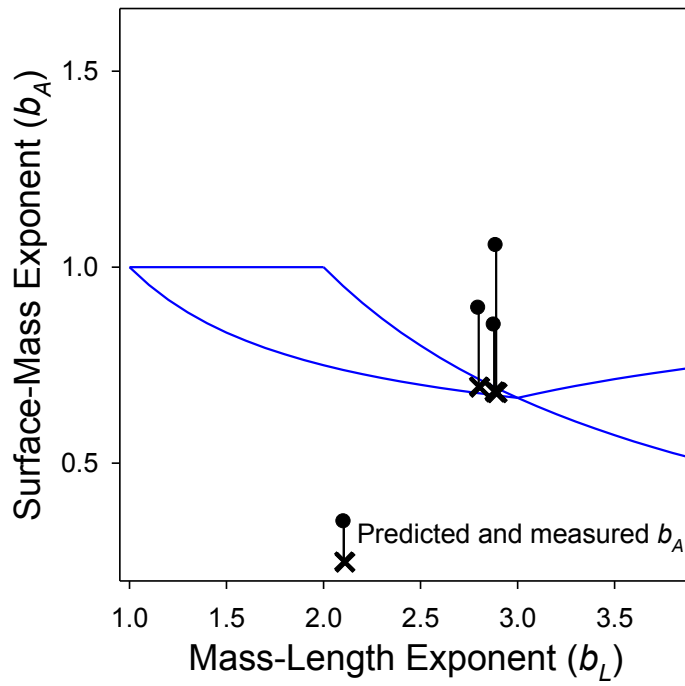
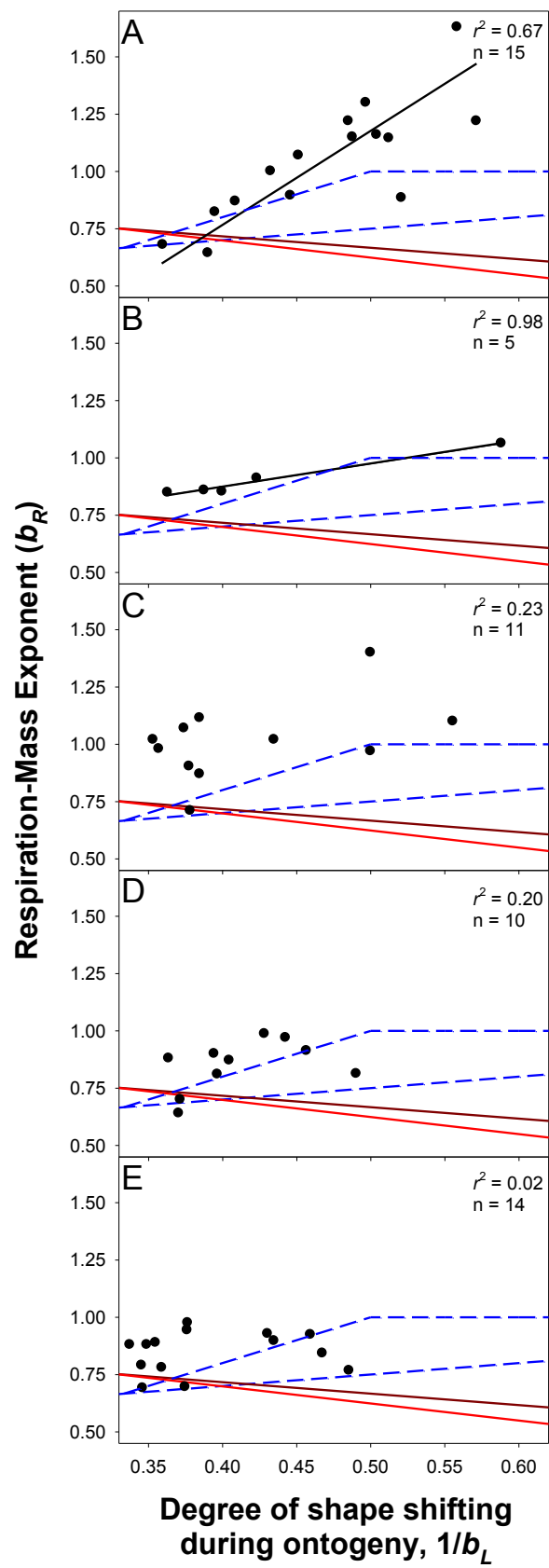


Fig. 4



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577 Fig. 5